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STUDIES ON JAMAICAN HYMENOPHYLLACEAE

FORREST SHREVE

(WITH EIGHT FIGURES)

The Hymenophyllaceae, or filmy ferns, are one of the most hygrophilous groups of terrestrial plants, and possess a number of features of anatomy and physiology in common with aquatics and the bryophytes. Although mainly restricted to tropical and subtropical regions with heavy rainfall and to habitats of high humidity, yet some of the species grow as epiphytes in company with bromeliads and succulent orchids, a fact which attracted the writer to a study of their local distribution and the gross physiology of their relation to water supply and atmospheric humidity.

The results presented in this paper were secured at the Tropical Station of the New York Botanical Garden at Cinchona, Jamaica, chiefly during the spring of 1906, while the writer was holding the Adam T. Bruce Fellowship in the Johns Hopkins University, and partly in the summer of 1909 during several months' absence from the Desert Laboratory. Cinchona is at an altitude of 1525 m. and is hard by the virgin rain forest, in which the Hymenophyllaceae attain to a wealth in species and individuals which cannot be far surpassed in any other place in the world. Of the 459 species credited to the family by CHRISTENSEN in the *Index Filicum*, 49 occur in Jamaica, and 34 of these have been available for study and observation.

Distribution

VERTICAL AND REGIONAL DISTRIBUTION IN JAMAICA.—JENMAN[1] lists for Jamaica 23 species of *Hymenophyllum* and 26 of *Trichomanes*. For 31 of the total number of species he states the vertical distribution as based on his long experience in collecting in various parts of the island. His statements indicate that there are but 5 species found only below 915 m. altitude, and 17 found only above 1220 m. The number of species (of the 31) to be expected at the different altitudes is as follows:

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[1] JENMAN, G. S., Synoptical list of Jamaican ferns. Bull. Bot. Dept. of Jamaica, nos. 18 and 20. 1890.

305 m.	610	915	1220	1525	1830	2135
10	19	19	21	31	27	20

It is in the unbroken forests of the windward slope of the Blue Mountains, at about 1525 m. altitude, that the Hymenophyllaceae are richest in species, and it is there too that they are most numerous in individuals. forming a far more conspicuous element of the vegetation than at higher or lower elevations. The most abundant and characteristic species at 1525 m. are:

Hymenophyllum fucoides Sw.[2]
Hymenophyllum asplenioides Sw.
Hymenophyllum ciliatum Sw.
Hymenophyllum polyanthos Sw.
Hymenophyllum lanatum Fee
Hymenophyllum axillare Sw.
Hymenophyllum lineare Sw.
Hymenophyllum sericeum Sw.
Hymenophyllum catherinae Hook.
Trichomanes crispum L.
Trichomanes rigidum Sw.
Trichomanes crinitum Sw.
Trichomanes radicans Sw.
Trichomanes pyxidiferum L.
Trichomanes capillaceum L. (*T. trichoideum* Sw.)

In virgin forest along the banks of the Mabess River, at about 1100 m. altitude on the windward side of the island, the writer has seen rich growths of Hymenophyllaceae, which were made up, however, solely of *Trichomanes Hookeri* Presl. (*T. muscoides* Sw.) and *T. pyxidiferum* L. Near the summit of Mount Diablo, at 600 to 700 m. altitude in the central limestone district of Jamaica, the Hymenophyllaceae are relatively rare, and must be sought carefully to be found at all. The only species observed there by the writer were:

Hymenophyllum hirtellum Sw.
Trichomanes Hookeri Presl.
Trichomanes sphenoides Kze.
Trichomanes crispum L.
Trichomanes arbuscula Desv. (*T. Bancroftii* Hook. & Grev.)

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[2] The nomenclature used is that of CHRISTENSEN'S *Index Filicum*. The writer's collection of Hymenophyllaceae was determined by the late Dr. L. M. UNDERWOOD of Columbia University.

The writer has been told by Mr. WILLIAM HARRIS that in collecting at Dolphin Head, in the extreme west end of Jamaica at 550 m. altitude, he observed only two species:

Trichomanes sphenoides Kze.
Trichomanes arbuscula Desv.

On passing upward in the Blue Mountains from 1525 m., the Hymenophyllaceae are found to become fewer in both species and individuals. There is but a single form found only above 1830 m. (*Hymenophyllum antillense* Jenm.), while other species common and characteristic above this altitude are:

Hymenophyllum tunbrigense Sm.
Hymenophyllum fucoides Sw.
Hymenophyllum asplenioides Sw.
Hymenophyllum polyanthos Sw.
Hymenophyllum lineare Sw.
Hymenophyllum lanatum Fee
Hymenophyllum hirsutum (L.) Sw.
Hymenophyllum sericeum Sw.
Trichomanes crispum L.
Trichomanes pyxidiferum L.

Judging by the ten-year rainfall record[3] for Blue Mountain Peak (2264 m.) and by hygrograph records obtained by the writer at Sir John Peak (1890 m.), the conditions of rainfall and humidity are no less favorable for the filmy ferns at the higher altitudes than at 1525 m.; indeed the percentage of cloudiness would appear from casual observations to be greater on the highest ridges and peaks. The mean annual temperature at Cinchona is 16° C., while that at Blue Mountain Peak may be closely approximated from a record of the monthly absolute maximum and minimum at that point to be 12° C. Although there are but few alpine features impressed upon the vegetation as a whole at the highest altitudes, yet the less abundance of the Hymenophyllaceae must be referred to the slightly lower range of temperatures rather than to less favorable conditions of rainfall and humidity. The scarcity of species and individuals at low altitudes and at such localities as Mount Diablo and Dolphin Head, in the drier portions of the island, is obviously due to the lower rainfall, humidity, and cloudiness as contrasted with the Blue Mountain forests. Where Hymenophyllaceae occur at all below 915 m., or upon the drier leeward slopes of the Blue Mountains at greater elevations than this, they are confined to spots where the conditions are made favorable by very local topographic or related causes; on rocks near to waterfalls, about the bases of trees in deep shade, and on the lower sides of moss-covered logs the conditions of humidity and water-supply resemble locally the climatic conditions of the mountain forests. The Hymenophyllaceae which occur at low altitudes are chiefly small species of *Trichomanes* which have a creeping rhizome and simple or pinnatifid leaves not exceeding 3 cm. in length. The forms which do not range above 914 m. are all of the description:

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[3] All climatological data for long periods are taken from the records of the Department of Public Gardens and Plantations of Jamaica.

Trichomanes punctatum Poir.
Trichomanes sphenoides Kze.
Trichomanes polypodioides L.
Trichomanes Krausii Hook. & Grev.
Trichomanes membranaceum L.

CLIMATIC CONDITIONS IN THE RAIN FOREST.—Some notion of the climatic conditions in the zone of maximum occurrence of the Hymenophyllaceae may be had from the series of records kept at Cinchona since 1871. The position of Cinchona on the leeward slope of the main ridge of the Blue Mountains, together with the exposure of the instruments in an open lawn, keeps this record from giving a full indication of the moistness of the rain forest itself. The writer judges from personal experience that the rainfall is between 20 and 30 per cent greater and the number of rainy days between 10 and 15 per cent greater in the forests than is indicated in the following figures for Cinchona:

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Rainfall . . .	7.26	4.09	5.32	6.36	11.10	8.00	3.89	8.29	9.22	18.57	12.32	11.11	104.77
Ry. days . .	14.1	12.5	12.8	12.9	18.1	13.5	10.8	11.2	16.1	21.4	18.3	16.2	179.4
Humid. . . .	84.1	83.1	83.9	83.4	85.2	84.8	79.6	80.4	84.4	88.9	86.0	86.3	84.1

In the course of some general work on the Blue Mountain region not yet published, the writer had occasion to expose a combined thermograph and hygrograph in a number of localities, and the record sheets figured herewith give a graphic conception of the daily march of temperature and humidity under natural forest conditions. The instrument was supported on an open framework one meter above the ground and sheltered by a canvas cover spread widely above it so as to keep off rain but permit a good circulation of air. The sheet shown in fig. 1 was obtained in the forest at New Haven Gap during the week of April 16–22, 1906, and that in fig. 2 in a clearing in the forest about 200 m. distant during the preceding week. The weather of the two weeks happened to be

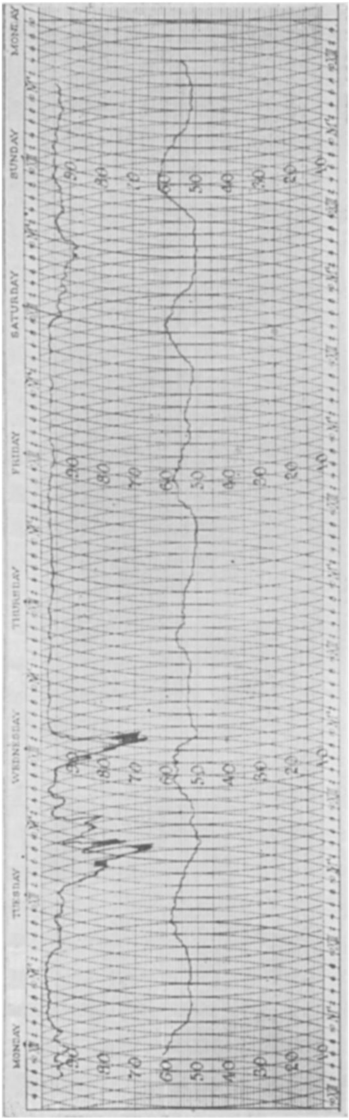

FIG. 1.—Record of temperature (the lower trace) and humidity on the floor of the rain forest at 1725 m. altitude.

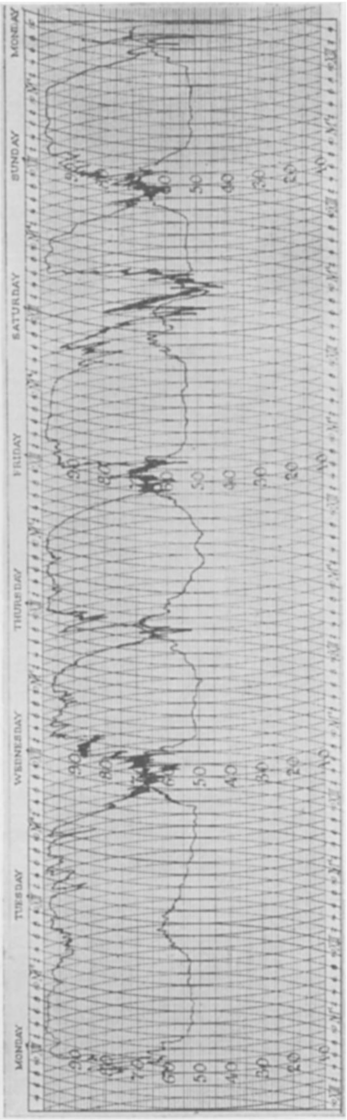

FIG. 2.—Record of temperature and humidity in a clearing in the rain forest at 1725 m. altitude.

closely similar, and the difference in the curves of humidity brings out strikingly the degree to which the conditions on the forest floor differ from the general climatic conditions of the region. Epiphytic vegetation in the canopy of the forest is subjected to fluctuations in humidity similar to those of the clearing, together with the slightly higher range of temperatures. The high and constant humidity conditions indicated in fig. 1 are characteristic of the deep forests of ravines and lower slopes throughout the Blue Mountain region from 1200 m. to the highest peaks, while the more open forests of the upper slopes and ridges have a climate approaching more nearly that of the opening.

LOCAL DISTRIBUTION OF THE HYMENOPHYLLACEAE.—SCHIMPER[4] has pointed out the distinctness in the character of the epiphytic vegetation near the forest floor and in the tops of the highest trees as observed by him in the forests of Trinidad and Venezuela. There the lowest epiphytes in the forest are tender hygrophilous plants which show no structural adaptations to the epiphytic habit and are often found as terrestrial plants. On the higher limbs and twigs of the largest trees are found xerophilous and succulent epiphytes possessing marked specialization in structure and in the ecology of reproduction. The Jamaican rain forest region has a highly developed erosion topography. Only in the ravines does the vegetation approach the stature and luxuriance of such lowland forests as were visited by SCHIMPER, and in them may be observed the same contrast in the character of the epiphytic vegetation. On the slopes, ridges, and peaks the forest trees are not so tall by one-half as in the ravines, and the canopy is much more open, particularly on the ridges and peaks. This results in the forests of the upper slopes being devoid of the epiphytes of the lowest levels of the ravine forest, while on the ridges and peaks the epiphytes which are characteristic of the canopy of the ravine forest may be found growing down to the forest floor. In other words, the trees of the upper slopes have the same epiphytic flora that would be found in the upper two-thirds of the trees of the ravines, while the trees of ridges and peaks have only those that are characteristic of the uppermost third, and the mid-height species are restricted in these habitats to the sides of prostrate trunks or fallen logs. These facts concerning the epiphytic vegetation in general are the key to the local distribution of the Hymenophyllaceae; the most important factors governing their distribution are those that have to do with the vertical differences in climate in the rain forest.

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[4] SCHIMPER, A. F. W., Die epiphytische Vegetation Amerikas. Bot. Mit. aus den Trop. Heft. 1. 1888.

The commonest filmy ferns that are invariably rooted in the soil on the floor of the forest are *Trichomanes rigidum*, *T. radicans*, and *T. scandens*. The first of these has a short erect rootstock and its cluster of stiff leaves grows to a height of 20 cm. It is found on the floor of deep ravines or elsewhere in dense shade, and its constant wetness is well attested by the growths of epiphyllous hepatics which cover all but the youngest leaves. *Trichomanes radicans* is a climber, sometimes reaching as much as 2 m. from the ground, but only in the most moist situations. Like the foregoing species it has finely dissected leaves, the branches of which are winged with upturned leaf tissue, providing it with a ramifying system of gutters, which happen to serve well in distributing over the leaf the chance drops of water which fall from overhanging foliage.

There are a number of facultative epiphytes with erect leaves which either grow in clusters out of an erect rootstock or are spaced along a horizontal rhizome. These do not often grow in the soil itself, but are commonly found on the ground rooted in tufts of moss, on fallen logs, or on the bases of the trunks of trees. These forms are slightly tolerant of the drying off of their leaves, but they are never found over about 2 m. from the ground except in the deepest ravines. The habit of the leaves being erect, their wetting must take place from rainfall or the dripping of wet foliage; their roots, however, are very favorably situated as respects water supply. The common members of this category are: *Hymenophyllum abruptum*, *H. ciliatum*, *H. microcarpum*, *Trichomanes Hookeri*, *T. pyxidiferum*, and *T. capillaceum*. *Trichomanes capillaceum* has the most delicately cut leaves of any of the Jamaican species; and its commonest habitat is the bases of the trunks of tree ferns, where it is rooted among the coarse rhizoids of the tree fern and is usually shaded and sprinkled by the overhanging leaves of the climbing fern *Lomaria attenuata*. *Hymenophyllum asplenioides* is quite as closely restricted to the most moist habitats as are any of the above-mentioned species, but the fact that its leaves are pendant confines its occurrence to tree trunks and rocks.

Another group of species may be characterized, which are not sharply separable from the last, but are on the whole much more capable of enduring desiccation and insolation. They are never found on the floor of the forest in ravines nor as low-growing epiphytes there, but are mid-height epiphytes in ravines and are found on the lowest layers of the slope forests. Their leaves are erect and glabrous, growing singly along a creeping rootstock and not exceeding 10 cm. in length in any species. These are *Hymenophyllum polyanthos*, *H. fucoides*, *H. catherinae*, *H. tunbrigense*, and *Trichomanes crispum*. *Hymenophyllum polyanthos*

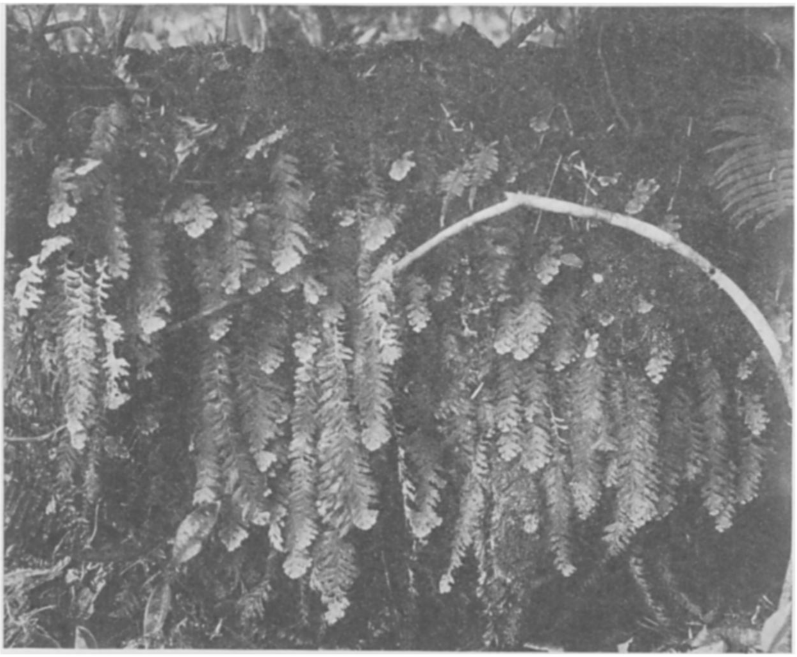

FIG. 3.—A typical colony of *Hymenophyllum sericeum*, pendant from a horizontal limb bearing mats of *Ptilidium*; one-fourth natural size.

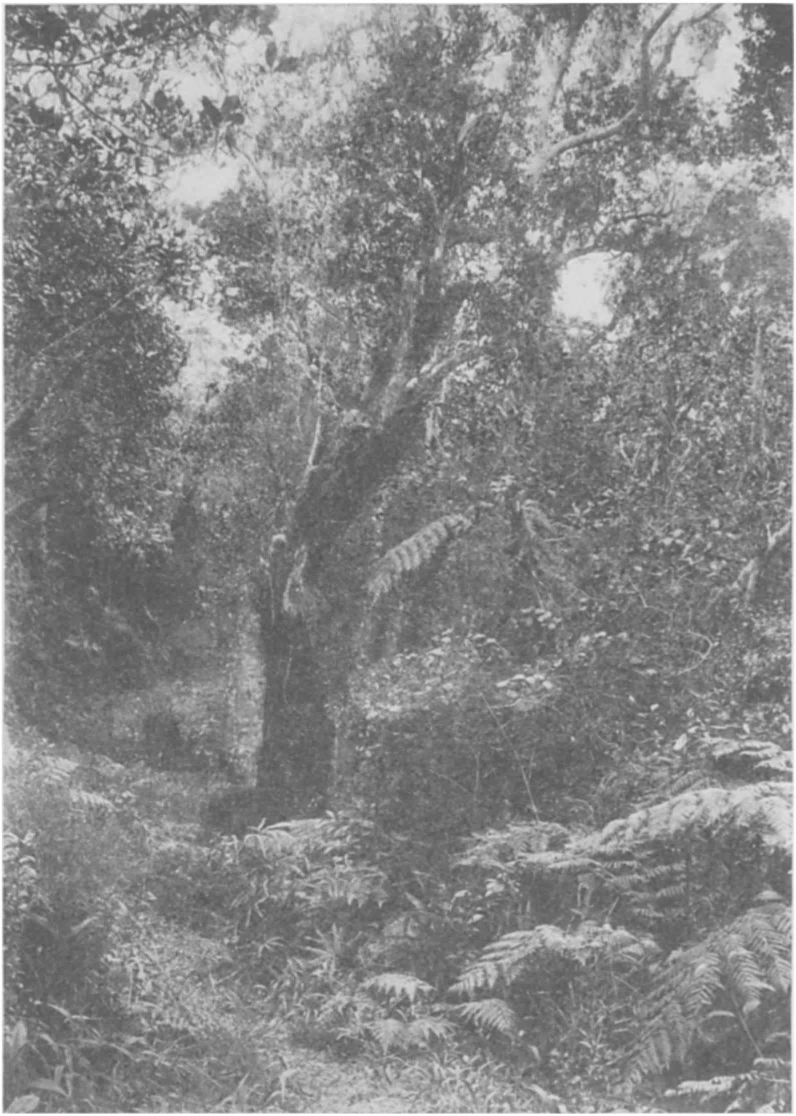

FIG. 4.—A tree in the drier rain forest of the leeward slopes of the Blue Mountains, with epiphytic colonies of *Hymenophyllum sericeum* growing up to 6 m. from the ground.

is the commonest filmy fern in Jamaica, and, with the exception of the hairy forms to be mentioned, it is the most capable of resisting desiccation of any of the species. On losing water its pinnae curl downward and the midrib itself then curls, so that the whole leaf tends to close into a form resembling the circinate shape of a young leaf. *Hymenophyllum fucoides* and *H. catherinae* have also characteristic modes of curling up on becoming relatively dry. The writer has seen the rain forest on exceptionally bright days, when the humidity had fallen to 60 per cent, when every plant of these three species was curled in a marked degree. The curling is not at all in such a manner as serves to protect any part of the leaf from further desiccation.

The three pendant hairy forms *Hymenophyllum sericeum*, *H. lanatum*, and *H. hirsutum* are the most resistant to drying and insolation of any of the filmy ferns. Their pendant habit confines them to the sides or bottoms of logs and leaning trunks, and they are most flourishing just beneath large clumps of mosses and hepatics, which serve as reservoirs from which supplies of water may be secured for several days after a rain. *Hymenophyllum sericeum* is not common in the topmost limbs of trees, probably through the lack of the moss substratum, but it grows in situations where it must often be subjected to two or three hours of sunshine on clear days, and it sometimes occurs as much as 12 m. above the ground in slope forest (figs. 3, 4). As the leaves grow the old pinnae die off, so that it is not an uncommon thing to find a naked rachis 30–40 cm. long with a dozen pairs of young pinnae at the tip. There are two hairy pendant species of *Trichomanes*, *T. lucens* and *T. crinitum*, but they are not at all resistant to desiccation. They are almost confined to the under sides of rotting logs, where they are rooted in the log itself and sheltered from rain and the drip from foliage. The writer has seldom seen wet leaves in nature in either of these species, both of which have a metallic gray-green color. Their physiology has not been investigated.

Physiology

ROOT-ABSORPTION.—In order to test the ability of the various species of Hymenophyllaceae to secure by root-absorption all the water required in a humid atmosphere, a number of individual plants or clumps of plants with undisturbed substratum were brought into the laboratory and the leaves allowed to dry off, but not to curl through too great loss of water. The plants were then placed under bell jars in which the humidity was kept above 90 per cent, and the roots wetted every day or two without wetting the leaves. It was not necessary to take any precautions against condensation of moisture on the leaves, for whenever the atmosphere in the bell jars approached saturation there was immediate condensation on the cool walls of the jar, lowering the humidity. The following data record the result of this test:

Trichomanes rigidum lost turgor in 5 days; dead in 14 days.
Trichomanes radicans remained normal for 40 days, with the chloroplasts on the lateral walls.
Hymenophyllum microcarpum remained nearly normal for 40 days, some groups of cells having become disorganized.
Hymenophyllum ciliatum remained normal for 40 days.
Trichomanes capillaceum remained normal for 40 days.
Hymenophyllum asplenioides remained normal for 40 days.
Hymenophyllum polyanthos remained normal and grew for 40 days.
Hymenophyllum sericeum remained normal and grew for 40 days.

The only form in this series incapable of maintaining its turgidity (*Trichomanes rigidum*) has already been stated to be one of the most hygrophilous, and those capable of growing under the conditions of the experiment the least hygrophilous of the Jamaican species. The extremely low water loss from surface-dry leaves in a very moist atmosphere can be met, therefore, by root-absorption and conduction in all but the most pronouncedly moisture-loving species. There are certainly no other common species which rank with *Trichomanes rigidum* in this respect; even the extremely delicate *T. capillaceum*, also requiring the most moist habitats, when kept subsequently under the conditions of this test maintained a normal condition for 35 days, at the end of which time the experiment had to be discontinued.

The conduction of root-absorbed water to the leaves is through a vascular system very poorly developed as respects the number and size of the water vessels, and the path of the water from the veins of the leaf to the transpiring cells lies through other cells, perhaps only as many as 4 or 5 in the finely dissected forms, but as many as 10 in *Trichomanes crispum* or 25 in the simple leaves of *Trichomanes Hookeri.* In *Trichomanes rigidum* the number of walls between the vessels and the marginal cells is 6–8, but an examination of the lateral walls shows them to have a peculiar thickening, which gives the central part of each one as seen in section the appearance of having a double convex lens inserted in it (fig. 5). These ridges occur in the lateral walls throughout the leaf, so as to provide the leaf with a rigid meshwork which is calculated to strengthen it in very much the same way that a piece of wire glass is strengthened by the wire netting imbedded in it. Although at every point in the lateral walls there are areas of thin wall above and below the thickening, yet it can be readily seen that the thickenings serve to hinder the transfer of water from cell to cell, and may be accountable for the inability of this species to secure root-absorbed water quickly enough to meet even the demands of transpiration in a nearly saturated atmosphere. Although *Trichomanes capillaceum* is quite as hygrophilous a form as *T. rigidum*, it has to its advantage as respects water movement in the leaf the fact that its marginal cells are never more than 4 or 5 cells removed from the veins, and also that in its slightly thickened walls there are intercellular passages, capable of functioning as avenues for the ready transfer of water.

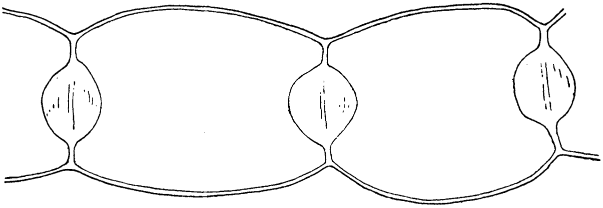

FIG. 5.—Vertical section of the leaf of *Trichomanes rigidum*, to show the mechanical thickening of the lateral walls; ×764.

TRANSPIRATION.—For the measurement of transpiration in the Hymenophyllaceae the only method available is that of the potometer, which admits of having the leaf surface wet or dry. Attempts to use entire plants on the potometer were not satisfactory, and the slenderness of the petioles of most forms, together with the smallness of the leaves in others, excluded from use all but *Trichomanes crispum*, *T. radicans*, and *T. rigidum*. Similar mechanical difficulties made it impossible to investigate the root pressure, so it is not possible to state what relation the facts ascertained by the potometer method as to the intake of water by transpiring leaves may bear to those which hold true for intact plants in a state of nature. In plants in which the transpiring surface is also capable of absorption, and in which there is no structural nor functional means by which transpiration is limited or regulated, it is to be expected that the rate will be largely a function of the conditions governing evaporation.

A single leaf of *Trichomanes crispum*, freshly cut from the plant and mounted on the potometer, was placed under a bell jar and kept wet by a drip from an opening in the top of the jar. There was no forward movement of the bubble in the potometer tube during the nine hours through which the test was run. In one of the two repetitions that were made there was a backward movement of the bubble at the rate of 1 mg. per hour during the early afternoon, suggesting a backward movement of water in the vessels due to the absorbing activity of the leaf surface. In order to compare the behavior of leaves only partially wet, the test was repeated so as to have the leaf wet at the start but without drip to keep it so. The following figures are the total losses in mg. for the intervals indicated:

11:00 A.M., leaf partly wet...............	
12:15 P.M., leaf just dry..................	73.5
1:15 P.M., leaf beginning to curl..........	61.0
1:16 P.M., leaf wetted again..............	
2:45 P.M., leaf beginning to dry off.......	4.0

Similar results were obtained with *Trichomanes radicans*. Neither in the dull diffuse light used in all other experimentation with the Hymenophyllaceae nor in bright diffuse light did thoroughly wet leaves show an intake of water through the petiole. A single test was made with a partially dry leaf of this species. The leaf had been mounted on the potometer since 9:00 A.M. and kept wet until evening. At 5:30 P.M. the drip was stopped and the bell jar left over the leaf during the night. At 9:00 the next morning the leaf was partly dry, but not sufficiently so for the tips of the pinnae to have begun to curl, and the basal pinnae were still wet. The intake of water during the 15½ hours was 39 mg.

The backward movement of the bubble in the test with *Trichomanes crispum* suggested determining the behavior of a leaf kept completely wet for several days. *Trichomanes rigidum* was used in this experiment, and in order to prevent any portion of the leaf from becoming dried the whole was submerged under a watertight bell jar in the manner shown in fig. 6. The following figures show a continuous and uniform retreat of the potometer bubble:

		Readings	Amts. per hr.
Oct. 31,	10:50 A.M.	65.5	
Oct. 31,	2:15 P.M.	63.5	0.60
Nov. 1,	9:00 A.M.	59.5	0.24
Nov. 1,	3:00 P.M.	57.8	0.26
Nov. 1,	6:00 P.M.	57.0	0.26
Nov. 2,	9:00 A.M.	54.0	0.20
Nov. 2,	12:00 noon	53.0	0.33
Nov. 3,	10:00 A.M.	47.3	0.26
Nov. 3,	12:00 noon	46.5	0.40
Nov. 3,	3:15 P.M.	45.5	0.30
Nov. 3,	6:15 P.M.	44.5	0.33
Nov. 4,	9:00 A.M.	40.5	0.27
Nov. 4,	12:00 noon	39.5	0.33
Nov. 4,	3:00 P.M.	38.5	0.33

That the pressure of the water surrounding the leaf had to do with this retreat is scarcely probable, in view of the hourly rate at night being always less than by day. While an intake of the amount here observed would be impossible in intact plants without exudation at the roots, the experiment gives an excellent demonstration of the absorbing power of the leaves, and the greater amounts absorbed by day than by night point to an influence exerted by photosynthetic activity on the absorption rate.

The extreme slenderness of the petioles of the ferns most capable of resisting surface dryness made it impossible to experiment with them on the potometer, but the experiments on root-absorption indicate that those forms are capable of maintaining a regular transpiration rate when atmospheric conditions do not make it too rapid.

The work of POND[5] and the more recent work of THODAY and SYKES[6] goes to show that submerged aquatics absorb, and presumably exude, considerable quantities of water. Each of the two methods employed by POND showed absorption by the normal root system; the method of THODAY and SYKES showed an intake by cut shoots. The writer has not made any experiments with the Hymenophyllaceae to ascertain if intact plants absorb with their uninjured root system when the leaves are wet or submerged. No evidence can be given, in other words, which is as satisfactory as that of POND for *Ranunculus aquatilis*. THODAY and SYKES showed a rapid intake of eosin solution by the cut ends of shoots of *Potamogeton*, and, if the eosin method may be trusted, their experiments go to show that the transpiration stream is quite strong even when shoots are severed from the root system. As respects

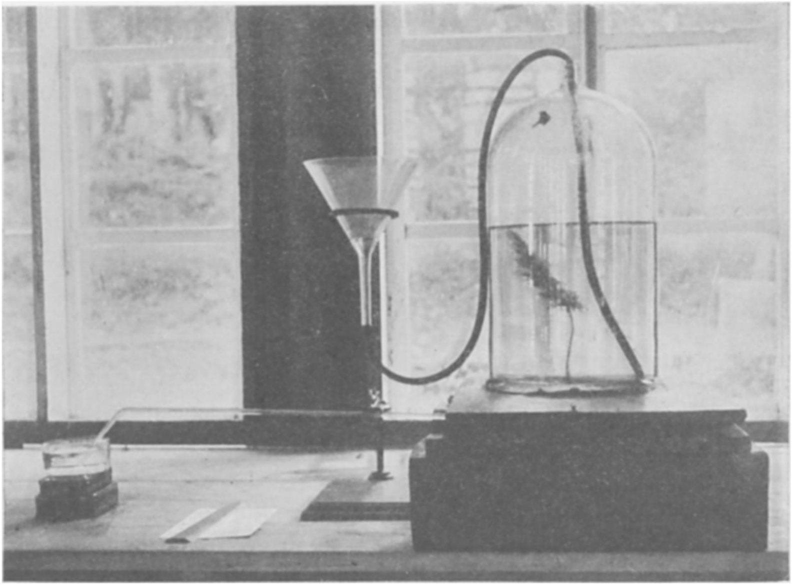

FIG. 6.—Form of apparatus used in determining the rate of leaf-absorption of water.

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[5] POND, RAYMOND H., The biological relation of aquatic plants to the substratum. Report U.S. Fish Comm., pp. 483–526. 1903.

[6] THODAY, D., and SYKES M. G., Preliminary observations on the transpiration current in submerged water plants. Annals of Botany **23**:635–637. 1909.

method, the writer's experiment with a single leaf of *Trichomanes* is comparable with those of THODAY and SYKES with severed shoots of *Potamogeton*. In spite of the violence which is done to the normal functioning of the leaves of flowering plants by removal from the plant (which will be shown below not to hold true of the filmy ferns), the writer is inclined, on the concordant evidence of the potometer experiments described, to believe that there is a standstill in the transpiration stream of a filmy fern when the leaves are wet. In exact analysis it is unthinkable that there should not be a simultaneous loss and intake of water through the leaf surface, but the backward movement of the potometer bubble shows that the absorbing activity is greater than the exudation when leaf-absorption is given play through the removal of the roots. In the intact plant, however, leaf-absorption is devoted solely to the maintenance of leaf turgidity, and the movement of root-absorbed water toward the leaves is in abeyance. When in its natural habitat, the filmy fern is now under aquatic conditions, now under those of a land plant. There may or may not be a transpiration stream in a plant according to the state of wetness of its leaves, and when the leaves are dry the ensuing root-absorption will or will not be able to meet the demands of water loss in the leaves according to the species and the humidity conditions in which it is placed. From the evidence given it appears that in nature there is now a slight transpiration stream in a given plant and now an intake of water by the leaves, accompanied by a cessation of conduction in the vessels.

TOTAL SUBMERGENCE.—A completely wet filmy fern is in a state equivalent to that of a submerged aquatic, excepting that it is under much more favorable conditions as respects the aeration of the water surrounding it. In order to determine what would be the effect of the stoppage of the transpiration stream for a considerable period, a number of plants were grown in total submergence, and in order to make these conditions as natural as possible the water was changed every four days and was aerated twice daily by injecting a fine stream of water with a large pipette. Flourishing individuals of the following species were selected, with their roots intact: *Trichomanes rigidum*, *T. radicans*, *T.*

crispum, *T. capillaceum*, *Hymenophyllum hirsutum*, *H. polyanthos*, and *H. sericeum*. At the close of 30 days of submergence these were all thriving, and the contents of the cells were of normal appearance under the microscope, save in the case of *H. sericeum*. Its leaves were blackened and the chloroplasts disorganized and lumped together. This most drought-resisting of the forms worked with (the one which is least often completely wet in nature) is therefore the only species incapable of assuming an aquatic rôle and having its transpiration stream stopped. Simultaneously with the above experiment, in which cistern water was used, an attempt was made to grow the same species in SACHS's nutrient solution, diluted to half-strength, with fatal results to all of the cultures within the first week.

ABSORPTION OF ATMOSPHERIC MOISTURE.—In the experiment regarding root-absorption, in which plants were kept with dry leaves in a moist atmosphere, it appeared possible that the survival of the individuals used might be in part due to the absorption of atmospheric moisture by the leaves. A test was made in which 10–15 leaves were cut from each of several species, sealed at the cut ends with vaseline, and dried at 70–80 per cent humidity until all the surface water was gone and the segments had just begun to curl. These were then laid on non-absorbent paper and placed in a small chamber kept moist with wet sheets of filter paper and clumps of sphagnum. The humidity was kept continually above 95 per cent, and was usually nearer saturation. Several pieces of iron that happened to be available were placed inside, and together with the glass top to the chamber served to catch the condensation whenever the humidity approached saturation. Although an effort was thus made to prevent actual condensation of moisture on the leaves, a slight amount of it may have taken place, but if it did it is no more than might have occurred in nature, and it failed to prevent loss of weight by some of the species used. The following series of weighings was made by removing the leaves from the non-absorbent paper and placing them between large watch glasses; as the humidity of the laboratory was seldom below 75 per cent, no great error was caused by the transfer. The first weight is that of the surface-dried leaves, the following ones being the weights on successive days while in the chamber. The chamber was accidentally opened one night, with a resulting fall in humidity that caused a loss of weight in all the leaves in it at the time, as indicated in the table by asterisks.

	Surface-dried weight	1st day	2d day	3d day	4th day	5th day	6th day	7th day
Trichomanes rigidum	1.510	1.308	1.293	1.317	1.290	1.260	1.165	1.115
Trichomanes radicans	3.880	3.500	3.210	3.015*	2.787	2.550	2.600	.....
Hymenophyllum asplenioides	0.460	0.430*	0.450	0.480	0.522	0.530	0.650	.....
Hymenophyllum polyanthos	0.317	0.350	0.402	0.458	0.350*	0.462	.....	.....
Hymenophyllum sericeum	0.668	0.755	0.840	0.861	0.914	0.930	.....	.....

Trichomanes rigidum and *T. radicans* showed themselves incapable of even so much as maintaining their original weight and became more curled each day, while the other species showed steady gains in weight and maintained a perfectly normal appearance. The fact that these species behaved differently under the same conditions, and that the gain or loss was consistently maintained in each case, together with the fact of their behavior being in accord with their habitat preferences, gives assurance of the result being indicative of their normal behavior. The more hygrophilous species, accustomed to being covered with a film of water, fail to maintain their turgidity even in the presence of a nearly saturated atmosphere, while the high epiphytes, to one of which at least constant wetness is fatal, gain appreciable quantities of water.

In order to determine whether the hygroscopic activity of the leaves of the epiphytic species was merely a physical phenomenon, several leaves of *Hymenophyllum sericeum* were killed in chromacetic fixing fluid for 24 hours, washed for 24 hours, surface-dried, and proceeded with just as the living leaves had been. The following figures were obtained simultaneously with gains in living leaves in the moist box:

	Surf. dry wt.	1 day	2 days	3 days	4 days	5 days	6 days
Hymenophyllum sericeum	0.621	0.560	0.510	0.505	0.490	0.428	0.410

In case the chrom-acetic fluid might have altered the hygroscopic character of the cell walls, the same test was repeated with corrosive sublimate as the killing agent, and the same kind of result obtained. The leaves of *Hymenophyllum polyanthos* were also killed and carried through the moist chamber, with closely similar results.

An attempt was made to determine whether the hairy covering on the leaves of *Hymenophyllum sericeum* and related species performs any function in connection with water supply or conservation. The hairs cover both sides of the leaf densely, are multicellular, and made up of a basal stalk upon which are jointed (4–7) hairs about 0.5–1 mm. in length, diverging from each other and parallel to the surface of the leaf. Both the basal stalk and the radiating hairs are hollow and devoid of living contents. In surface-dried leaves and those commonly gathered in the field, the hairs are filled with air. Leaves which were submerged, with all of the occluded air squeezed out from among the hairs, were found after 24 hours to have their hairs filled with water. On observing the access of water to empty hairs beneath the microscope, it was seen to enter them at once and rapidly, until only a small bubble of air remained, which persisted for several hours. When leaves in which the hairs had been completely filled with water by long submergence were surface-dried with filter paper and hung in the open air at a humidity of 80 per cent, they were found at the end of 1 hour and 20 minutes to have lost approximately half the water contained in the hairs. Of the amount lost it is more than probable that as much escaped by evaporation from the hairs as became available to the leaf cells. In other leaves which had empty hairs and which were placed in a very moist atmosphere the gains in weight were not accompanied by a visible accumulation of water in the hairs. It appears, therefore, that the leaf hairs do not serve as reservoirs of water either in sufficient quantity or for a sufficient length of time to be of importance in that rôle. The coating of hairs as a whole is capable of retaining externally an amount of water equal to twice the weight of the surface-dried leaf, and under the conditions of evaporation of the rain forest this external water might be retained for 5–10 hours. The writer has placed leaves under water without squeezing out the bubbles of air among the hairs, and found them still very imperfectly wetted up after 24 hours, and has watched dry leaves becoming wet during the commencement of rain in the forest, noticing that a heavy downpour of an hour's duration does not completely wet the leaves. It is a very uncommon thing even in the wettest weather to see leaves in the field which look saturated. The writer has no experimental evidence as to the possible rôle of the hairs in preventing water loss by the leaf cells themselves, but it is obvious that they do so to some extent, and also that they play a part in the ability of this species to withstand a greater amount of insolation than others do.

AUTONOMY OF THE LEAF AND ITS CELLS.—The extremely low degree of differentiation in the leaf tissue of the filmy ferns, and the fact that the same cells are at once capable of the functions of absorption, photosynthesis, and transpiration, seemed to indicate that the behavior of individual leaves when severed from the plant might be taken as a perfectly good criterion of their performance when *in situ*. As isolated leaves had been used in experimentation, it seemed desirable to determine their capacity for survival under the most favorable conditions. In order to do this leaves were taken from fresh plants of several species and hung in a moist chamber with wicks of cotton cord running from a pan of water so as to keep them constantly wet. The forms used were *Trichomanes rigidum*, *T. radicans*, *T. crispum*, *T. capillaceum*, *Hymenophyllum asplenioides*, *H. polyanthos*, and *H. sericeum*. At the end of 14 days all of these were in good condition, looking normal under the microscope, excepting *H. sericeum*, the inability of which to withstand submergence has already been noted. Its leaves had blackened and its chloroplasts become disorganized.

There being no reason to suppose that even portions of leaves would not survive equally well when removed from the whole leaf, a smaller series of leaf fragments was arranged, which were put in watch glasses of cistern water that was changed every other day. The only forms used were *Trichomanes capillaceum*, *T. rigidum*, and *T. crispum*, from each of which was taken a single pinna, a portion of a pinna 1 cm. long, and a portion 3 mm. long. The fragments were frequently examined under the microscope and were allowed to run for 50 days. Up to the end of that time the pinnae and the 1 cm. pieces were normal in appearance in all three species, excepting that in *T. capillaceum* the cells had become disorganized for two or three rows back from the cut ends. The pieces 3 mm. long failed to maintain normal condition.

These tests indicate that separate leaves are capable of surviving and maintaining normal appearance, and that portions of leaves are also capable of doing so provided they are not so small that the disorganization which takes place at the cut edges leaves only two or three rows of cells along the center that might be expected to survive. So far as concerns the vegetative functioning of the plant, the leaves are quite independent of each other, and, when the leaf is completely wet, the individual cells are as independent as are those of a colonial alga.

The water by which the leaves of the Hymenophyllaceae are bathed in nature is usually rain water that has either fallen directly upon them or has dripped from foliage that has already been washed clean by frequent rainfall, and is therefore not capable of carrying any mineral salts to the plant. The water which is available to the roots, however, has usually been for some time in contact with epiphytic colonies of moss and flowering plants, and with the rotting leaves and bark always to be found beneath clumps of epiphytes, and I assume that it is rather rich in salts, including nitrates. The water which drips down over the leaves of pendant species is the same as that available to the roots of other species.

Plasmolysis with NaCl gave the following values for the osmotic strength of the sap of a few of the common species: *Trichomanes rigidum*, *T. radicans*, *T. crispum*, and *Hymenophyllum sericeum*, 0.428 N; *Hymenophyllum asplenioides* and *H. elegantissimum*, 0.514 N.

THE CHLOROPLASTS.—The chloroplasts of the filmy ferns are spherical and somewhat smaller than in most other groups of ferns. In all the Jamaican species they lie normally in a single densely packed layer next the two outside walls of the leaf cells (fig. 7). There is rarely a difference in their abundance on the two sides of the leaf.

A paleness in the coloration of the leaves of *Trichomanes radi-*

cans frequently observed in the field was found to be due to a retreat of a large proportion of the chloroplasts to the lateral walls of the cells, a performance that was afterward noticed in experiments with this and other species when isolated leaves were surface-dried and kept without access of water in a moist chamber, and also in rooted plants of *Trichomanes rigidum* which were dry as to the leaves. On the presumption that illumination was the principal factor involved in the movement of the chloroplasts, plants of several species were placed in bright diffuse light and in direct sunlight, the fronds being kept quite wet in the first instance by keeping the plants under a bell jar, and in the second case by submerging them. The species used were *Trichomanes radicans*, *T. crispum*, *T. rigidum*, *T. capillaceum*, *Hymenophyllum sericeum*, and *H. hirsutum*. The first of these was the only species influenced. Under bright diffuse light for 2 hours, about one-third of the chloroplasts had gone to the lateral walls, and illumination for 4 hours sent one-half of them there. The influence of full sunlight was nearly identical. When all of the above-named species were placed in total darkness for 20 hours, the chloroplasts were found in their normal positions on the outside walls.

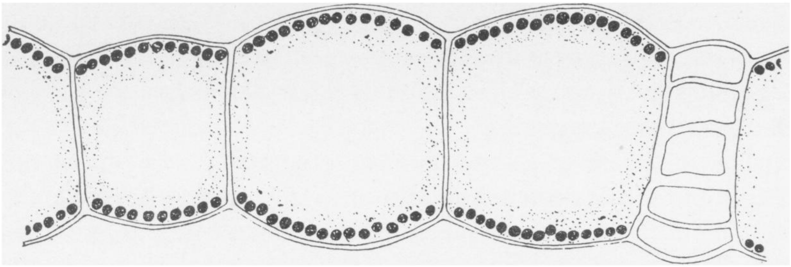

FIG. 7.—Vertical section of the leaf of *Trichomanes Hookeri*, to show the distribution of the chloroplasts and the size of the sap vacuole in a non-specialized form; ×764.

These tests serve to indicate that intense illumination brings about a movement of the chloroplasts only in *T. radicans*. Since it is found only in heavily shaded habitats, and since species in which there is no responsive movement in strong light are found to have a portion of their chloroplasts on the lateral walls when the surface is dry, it would appear that it is the dryness of the leaf surface rather than conditions of illumination that are responsible for the change of position of the chloroplasts.

Conclusions

The foregoing experiments have demonstrated that the filmy ferns may obtain water by any of three methods: root-absorption, leaf-absorption, and the absorption of atmospheric moisture by the leaves. By far the greatest mass of water intake is by leaf-absorption, root-absorption operating intermittently according to the wetness of the leaves. The high epiphytes are the only forms capable of availing themselves of atmospheric humidity, and the actual amounts of water thus obtained are small. The effect of a pronounced fall in humidity is to remove the water film from the leaves and to stop leaf-absorption; root-absorption is then taxed to a degree dependent on the lowness of the humidity and the duration of its lowness. Fig. 1 shows two drops in the humidity curve to below 70 per cent, neither of which lasted over 2 hrs., and it is probable that this trace, showing 4 hrs. of humidity below 70 per cent in the week, is representative of the average conditions of the floor of the rain forest.

When the surface of a leaf remains dry in a moist atmosphere, many, or even nearly all, of the chloroplasts will be found on the lateral walls of the cells. The duration of dryness necessary to bring this about varies from 3 or 4 hrs. in *Trichomanes rigidum* and other hygrophilous forms, to 8–10 hrs. in *Hymenophyllum polyanthos*. In the more hygrophilous species the removal is accompanied by a curling of the leaf, which is more a function of the humidity of the atmosphere than of surface dryness. If leaves are dried and suddenly placed in an atmosphere of 70 per cent humidity or less, the curling will take place before the movement of the chloroplasts. The movement appears to occur at times when there is no absorption of surface water taking place, but when there is a maintenance of the turgidity of the leaf by the movement into the leaf of root-absorbed water. The shifting of the chloroplasts appears, in other words, to be such as to place them opposite the walls through which the entry of water is going on.

When a gradual fall of humidity is experienced by surface-dry leaves, they assume withered shapes, and air bubbles appear in the cavities. If isolated leaves in this state are placed in a moist chamber, they will resume an appearance of turgidity within a few hours, and while the bubbles are still present in the sap. This false resumption of turgidity is therefore no more than the absorption of water vapor by the walls, and shows that the wetness of the walls rather than their distention by sap pressure is the cause of the turgidity of the leaves. The recovery of false turgidity is accompanied by considerable gains in weight, and these gains have already been shown to continue for several days. The absorption of atmospheric moisture is not great enough to replace the air bubbles in the cells when they have once appeared. Leaves of *Hymenophyllum polyanthos* with bubbles in the older cells have been kept for 5 days in a nearly saturated atmosphere without an appreciable diminution in the size or number of bubbles. The cells at the tip of the leaf and the tips of the terminal pinnae, which are richer in protoplasm, were at no time deprived of water sufficiently to have bubbles, and doubtless drew upon the supplies of water in the older cells.

The more hygrophilous species are not capable of withstanding a considerable loss of water from their sap cavities; while both *Hymenophyllum polyanthos* and *H. sericeum* have been found capable of withstanding very great losses. The extreme extent to which the lumen of the cells of *H. polyanthos* may be replaced by air is shown diagrammatically in fig. 8. The exposure of a dry leaf to sunshine for 30 min. or to very dry air (60–40 per cent) for an hour will suffice to bring about this condition. If the duration of the condition is not more than 1–3 hrs., the leaf will recover on being wet up, the chloroplasts (at first misplaced) will gradually (perhaps only after several days) resume their normal position, and the leaf will survive. A less degree of vacuolation of the leaf cells can be withstood for a longer time, but repeated attempts have shown it impossible to obtain any very exact measure of the behavior of leaves in this respect.

The physiological behavior of the Hymenophyllaceae in respect to their capacity for enduring the loss of water from the sap vacuoles of their cells is similar to that of many xerophilous mosses, hepatics, selaginellas, and ferns. The filmy ferns are not capable of enduring as complete a removal of water as are the other archegoniates mentioned, but in view of the extremely hygrophilous character of most members of the family, it is sufficiently noteworthy that the few species which grow as high epiphytes in the Jamaican forests are capable of enduring as great water loss as they are. Whereas several families of flowering plants have contributed to the epiphytic flora of the rain forest species which are of xerophilous structure, the Hymenophyllaceae have contributed a small group of species the xerophily of which resides not at all in their structure, but in the capacity of the protoplasmic utricle to withstand the removal of the sap which is its source of water and nutrient salts.

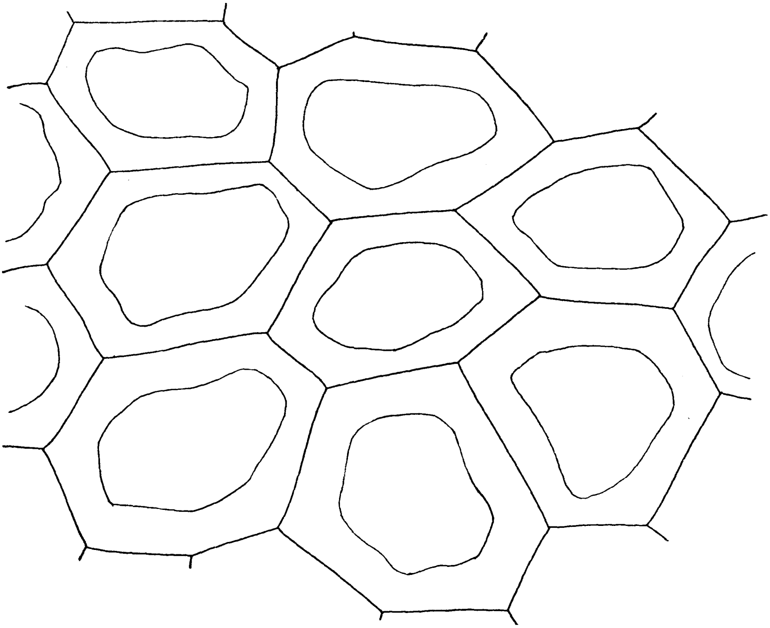

FIG. 8.—Diagram to show the maximum extent to which the sap cavities of the cells of *Hymenophyllum polyanthos* may be occupied by air bubbles in desiccated living leaves.

Summary

1. The Hymenophyllaceae are most abundant in species and individuals at about 1525 m. altitude.

2. The Jamaican species differ in their relation to moisture conditions from the most pronounced hygrophily to a relative degree of drought resistance.

3. The differences of climate from floor to canopy in the rain forest determine the local distribution of the different types of Hymenophyllaceae.

4. The low water loss from surface-dry leaves in a very moist atmosphere can be met by root-absorption in all but the most hygrophilous forms.

5. The transpiration current moves when the leaves are wholly or partly surface-dry, but is at a standstill when the leaves are thoroughly wet.

6. All but the most drought-resistant epiphytic species of Hymenophyllaceae are capable of living for considerable periods as submerged aquatics.

7. The drought-resistant species are capable of absorbing atmospheric moisture when surface-dried, if kept in very moist air.

8. Continued desiccation results in the loss of the water of the sap cavity of all mature leaf cells, recovery depending on the duration of the desiccation.

9. The relatively xerophilous epiphytic Hymenophyllaceae owe their ability to resist drought to the capacity of the protoplasmic utricle of the leaf cells both to survive the replacing of the sap cavity by air and also to lose a rapidly diminishing amount of water on continued desiccation.

10. The Hymenophyllaceae (structurally and physiologically a very distinct group of ferns) have developed forms capable of growing in relatively dry situations through possession of an intracellular or functional xerophily, much less pronounced than that possessed by many mosses and selaginellas, but like it in kind.

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